

On the behavior of vicunas (*Vicugna vicugna* Molina, 1782)

Differences due to sex, season and proximity to neighbors

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Abstract

Investigated the behavior of adult, territorial males and the associated females in a high-density population at the Pampa Galeras National Vicuna Reserve and a low-density population near Arequipa in the southern Peruvian puna comparing the breeding season (February–April) with the non-breeding season (August–September). Data were collected by the focal sample procedure using a 1-h observation period. Thirteen categories of behavior were used, “graze”, “lookup”, “alert”, “roll”, “lie”, “groom”, “walk”, “run”, “chase”, “defecate-urinate”, “threat”, “standoff”, and “nurse”. A time budget was used to compare behaviors under different conditions. The behavior of male vicunas during the breeding seasons was both quantitatively and qualitatively different than behavior displayed during the non-breeding season. Males performed all behaviors at a higher rate during the breeding season. The behaviors of females differed quantitatively between seasons. Hypotheses dealing with female cooperation and defense of resources were rejected. The proximity of neighbors affected the behavior of both males and females. Females spent more time in alert when neighbors were present, males grazed less and spent more time performing behavior associated with repelling intruders.

Introduction

Vicunas are ungulates (Family Camelidae) that inhabit the high-altitude andean puna. Their social organization is characterized by three types of social groupings: families that tend to remain resident in one area throughout the year, groups of bachelors that wander over a large area, and solitary males. Each family consists of a single adult resident male, one to several females, and young of the year. Resident males act agonistically towards other males and defend a territory year-around (KOFORD 1957; FRANKLIN 1974, 1978, 1983; BOSCH and SVENDSEN 1987). Breeding occurs over a well-defined period from late February through April (HOFMAN et al. 1983). The mating system is polygynous with about three females associated with each resident male. All indications are that females only mate with the resident male with which they are associated (KOFORD 1957; FRANKLIN 1974, 1978, 1983; MENARD 1982; HOFMAN et al. 1983; BOSCH and SVENDSEN 1987).

The objectives of this research were to describe the behavior of adult, resident male and female vicunas and to characterize similarities and differences between them, to quantify how behavior was influenced by season of the year (breeding season vs non-breeding season) and by density (high density vs low density), and to test two hypotheses dealing with the role of the female in the group (intragroup cooperation and defense of resources).

Material and methods

Populations

The study was carried out in the southern Peruvian puna. The density of the Pampa Galeras population (PG) at the Pampa Galeras National Vicuna Reserve, Department of Ayacucho, was about 0.5 per ha based on the 1980–81 census. The density of this population was sufficiently high so that

available pasture was occupied completely by resident territorial males and their associated females and young. Territories abutted one another and neighbors were always in view. Bachelor groups wandered over the area daily. The Coppermine population (CM) was located northeast of Arequipa, Department of Arequipa. The density was unknown, however it was sufficiently low so that available pasture was not occupied completely. Some families were isolated, and the borders to the territories of these resident males did not abut. Seven families in the CM population whose territory did not abut with the territory of others and whose nearest neighbors were usually out of sight were selected and are used in the analysis.

Seasons

Data were collected during two periods designated as the breeding season (March–April–May) and the nonbreeding season (August–September) in 1982 and 1983 (HOFMAN et al. 1983).

Observations

Observations were made in the relatively flat, treeless terrain with binoculars and data were recorded either in written field notes or with the aid of a tape recorder. Field work was restricted between sunrise and noon during March and April because of afternoon storms. After mid-April when afternoon storms ceased, observations were made throughout the day. Vicunas were classified as resident male (males holding a territory), bachelor male (nonresident males in bachelor groups), adult females, and young (BOSCH and SVENDSEN 1987). Only data collected on adult males and adult females were used in this analysis.

Behaviors

Thirteen categories of behavior were used. "Graze" included all feeding behavior. "Lookup" included all looking around except for the more intense "alert" in which vicunas looked with head raised and ears erect. "Roll" in the dirt was separated from "lie". "Groom" included scratching the body with either the forefoot or hindfoot as well as biting and chewing the fur. Locomotory categories included "walk", "run", and "chase". "Defecate-urinate (DU)" represented all elimination at dung piles or elsewhere. "Threat" was characterized by an erect body posture with ears laid back and head held high. The display by males interacting with one another at their territory boundaries was termed "standoff". Suckling by young was called "nurse". When a male directed movements of females in his territory, it was termed "herding".

Sampling

Time budgets were determined for individual resident vicunas using the focal sample procedure. All observations were made on residents while they were within the boundary of their home territory. A focal sample consisted of a 1-h observation period on a single vicuna, the duration of each behavior was recorded in seconds. Only data on resident males and females were included in this analysis. During the breeding season at Pampa Galeras, data were gathered on 23 vicuna families in a random manner. Different families were studied on different days throughout the week. During the following week, some families were resampled, some were not. Within a given day, vicunas from 2 to 5 different families were studied. A common procedure was to select a family and gather data on the male and 1 or 2 females, then move on to another family. There were sufficient vicuna families in the study area so that it was not necessary to gather data on the same family group repeatedly. Data for the nonbreeding season at Pampa Galeras were gathered on 8 different vicuna families. Seven different families were studied at the Coppermine site. A single focal sample was collected on each male and 1 or 2 of the females in each family. Each 1-h focal sample is treated as an independent sample in the analysis. The only criteria used for selecting a family to study was that it included a male and at least one female. The size of the families studied ranged from 2 to 7 ($\bar{y} = 3.9 \pm 1.97$). Data used to test the hypotheses were number of minutes of activity in a category of behavior per hour. Tests of various hypotheses were made using the Kruskal-Wallis test.

Results and discussion

Males vs females

Significant differences were found between males and females during the breeding season for all categories of behavior except "lie" (Tab. 1). Females spent more time in "graze", males more time in other categories of behavior (Tab. 2). Males spent significantly more time in "lookup" and "alert" than did females during the non-breeding season (Tab. 1),

Table 1. Time budget for behaviors of male and female vicunas during the breeding season (BR), and the nonbreeding season (NBR) at Pampa Galeras, Peru

Behavior category	Male		Female	
	BR	NBR	BR	NBR
Graze	2668 ± 516	2934 ± 252	3273 ± 252	3323 ± 176
Lookup	276 ± 199*	107 ± 74	85 ± 85	59 ± 31
Alert	206 ± 233	255 ± 261	28 ± 62*	66 ± 109
Lie	65 ± 204	75 ± 212	67 ± 200	21 ± 6
Roll	7 ± 14	2 ± 6	4 ± 10*	1 ± 4
DU	31 ± 26	27 ± 24	9 ± 13	12 ± 10
Walk	198 ± 158	179 ± 131	81 ± 77	76 ± 54
Run	40 ± 66*	3 ± 9	6 ± 13	2 ± 4
Chase	23 ± 32	11 ± 16		
Threat	4 ± 11	0	5 ± 20	0
Standoff	24 ± 94*	0		
Groom	15 ± 11*	4 ± 4	10 ± 12	6 ± 7
Nurse			25 ± 51	34 ± 63
	(N = 109)	(N = 8)	(N = 119)	(N = 20)

* significantly different between breeding and non-breeding seasons within sexes, Kruskal-Wallis ANOVA. N = number of 1 h focal samples. Data are given as mean and standard deviation.

whereas females spent more time in "graze" (Tab.2). Both sexes visited dung piles to defecate and urinate ("DU"), kneaded the dung pile with their forefeet, and smelled the kneaded dung. Males visited the dung piles about 3 times more frequently than did females during the breeding season and about 2 times more frequently during the nonbreeding season.

In polygyny, a male's reproductive success is limited by the number of females he mates with, whereas the reproductive success of females depends on her ability to rear offspring (GEIST 1971; TRIVERS 1972; CLUTTON-BROCK et al. 1979, 1980). The behavior of male and female vicunas reflects these different roles. Males engaged in behaviors associated with vigilance, territorial display, and chases, whereas females eat. Female vicunas grazed 91 % of the time they were observed and males grazed 75 % of the time (BOSCH and SVENDSEN 1987).

Behavioral differences were also evident in everyday activities such as "walk" and "DU" (Tab.2). Walk is the normal way in which vicunas move about during the day. During the breeding season, males spent significantly more time in "walk" than did females. Males walked to visit dung piles, to herd females, and to check out the territory boundary. Family members use communal dung piles at which they defecate and urinate. Males defecate and urinate at dung piles more frequently than do females (KOFORD 1957). FRANKLIN (1979, 1983) suggested that dung piles served as scent posts for the family members and were involved in maintaining the territory. The frequent visitation of dung piles by males in both the breeding and non-breeding seasons is consistent with the pattern of ter-

Table 2. Comparison of the behavior of male and female vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru

Values for each category are given in table 1

Behavior category	BR	NBR
Graze	M < F	M < F
Lookup	M > F	M > F
Alert	M > F	M > F
Lie	M = F	M = F
Roll	M > F	M = F
Walk	M > F	M = F
DU	M > F	M = F
Run	M > F	M = F
Groom	M > F	M = F

Significance level, $p < 0.05$, Kruskal-Wallis ANOVA.

ritoriality where cues related to maintaining the territory are present throughout the year. Dung piles may contain cues for individual recognition and reproductive condition of the female.

Males and females spent the same amount of time in "walk" during the non-breeding season, however the context in which "walk" occurred in each was different. Males spent less time interacting with neighbors and bachelors during the non-breeding season, but still visited dung piles and territory boundaries. Females spent their time walking and feeding. Total time spent in "walk" by females was greater in the non-breeding season. Perhaps this was related to the quantity and quality of forage available and reflected more time searching for food.

Male: Breeding season vs non-breeding season

Significant differences were found between seasons for categories of behaviors of males associated with increased vigilance, chasing, and displays at territory boundaries (Tabs. 1, 3). "Threat" and "standoff" were recorded only during the breeding season, all other behaviors were performed more frequently during the breeding season.

Table 3. Comparison of the behavior of male vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru

Values for each category are given in table 1

Graze	BR = NBR
Lookup	BR > NBR
Alert	BR = NBR
Lie	BR = NBR
Roll	BR = NBR
DU	BR = NBR
Walk	BR = NBR
Run	BR > NBR
Chase	BR = NBR
Threat	BR > NBR
Standoff	BR > NBR
Groom	BR > NBR
Significance level $p < 0.05$, Kruskal-Wallis ANOVA.	

Table 4. Comparison of the behavior of female vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru

Values for each category are given in table 1

Graze	BR = NBR
Lookup	BR = NBR
Alert	BR < NBR
Lie	BR = NBR
Roll	BR > NBR
DU	BR = NBR
Walk	BR = NBR
Run	BR = NBR
Threat	BR > NBR
Groom	BR = NBR
Nurse	BR = NBR
Significance level $p < 0.05$, Kruskal-Wallis ANOVA.	

Female: Breeding season vs non-breeding season

Females spent more time in "alert" during the non-breeding season, and more time in "threat" and "roll" during the breeding season (Tabs. 1, 4).

Male: Male interactions

Fighting among vicunas did not occur frequently enough to be recorded in the sampling periods. However, fights were observed at other times. No fights were observed among females or among resident males, all fights observed occurred between resident males and bachelor males. Injuries due to these fights cannot be determined, but headlong chases did result in spectacular falls by both the pursued and pursuer. Bachelor males were observed with broken legs, dislocated hips, and open wounds, some of these could have resulted from fights or falls during chases.

Herding and positioning by the male

Male vicunas often directed members of their family to move in a particular direction or to a location within the territory "herding". "Herding" occurred most often during the breeding season, but it also occurred during the non-breeding season and at the low density site. A herding male moved toward the females and young, using threat displays toward individuals. Females that strayed from the group were directed back. A hesitant female received a bite to the rump. Males herded females from the edge of the territory to the middle, especially when a neighboring male was nearby or following "standoff" at a boundary.

Males spent more time in vigilance during the breeding season than they did during the non-breeding season. This was reflected in the amount of time spent in "alert" and "lookup". As the group moved through their territories on their daily activities, proximity to different neighbors changed. During the breeding season, males tended to position themselves between their females and the closest neighboring male. The position of various males with respect to the position of their females and neighboring males was determined over a several day sampling period at Pampa Galeras. Out of 52 sightings taken during the breeding season, 39 males were situated between their females and the closest male and 13 were not ($\chi^2 = 13$, $P < 0.05$), whereas out of 21 sightings taken during the non-breeding season, the numbers were 13 and 9 respectively ($\chi^2 = 0.7$, ns).

Females: Group cohesion and defense of resources

Vicunas normally walk through their territory during daily activities. Females walk while feeding, walk to dung piles, and walk to different regions of the territory. Females sometimes remained together and moved in unison with the male to one side, and at other times they were spread out and each female moved independently from the others. When two females came too close to one another, one or both responded with "threat". Females did not engage in social behaviors such as allogroom. Even licking of the young by a mother was an extremely rare event.

When intruders trespassed on the territory, resident females did not rush to chase the intruders off as did the male. Females continued to graze unless the chase came close. If the intruder was a non-group female that was trying to join the group, the females investigated the newcomer, made threats towards her, but did not drive her off. Females did not engage in displays at the boundaries, nor did they show other behaviors that could be interpreted as defense of the territory.

A female should try to prevent other females from joining a group unless there are advantages due to cooperation (ALTMANN et al. 1977) or the females are related (HAMILTON 1964). Of the commonly cited advantages of group-living, only predator vigilance cannot be ruled out for female vicunas. Females performed no behaviors during the day that indicate cooperation in gathering food, defending resources, or caring for young.

Female philopatry characterizes group formation in many polygynous species of mammals (GREENWOOD 1980). Female young settle with or near their mother and may form matrilineal groups (ARMITAGE 1981). FRANKLIN (1978) reported that vicunas expelled female young after about 10 months of age. However, we observed female young still present in the family 24 months after birth, and young as old as 16 months were allowed to suckle. MENARD (1982) reported similar findings. We suggest that philopatry may be involved in the formation of the multifemale group, whereby females are able to increase their inclusive fitness by sharing the resources of a proven territory with female kin.

Table 5. Time budget for behaviors of male and female vicunas during the breeding season at the Coppermine site

Data are from 7 selected families without neighbors

Behavioral category	Male	Female
Graze	3015 ± 334	3397 ± 131*
Lookup	92 ± 36	38 ± 131*
Alert	140 ± 73	62 ± 68*
Lie	93 ± 222	36 ± 84
Roll	6 ± 10	3 ± 4
DU	36 ± 28	16 ± 26
Walk	205 ± 119	37 ± 24*
Run	5 ± 8	3 ± 7
Chase	2 ± 4	
Threat		
Standoff		
Groom	7 ± 8	9 ± 10
	(N = 7)	(N = 13)

* significantly different between males and females, Kruskal-Wallis ANOVA, significance level $p < 0.05$. N = number of 1 h focal samples. Data are given as mean ± standard deviation.

Table 6. The behavior of male and female vicunas in the breeding season, comparing vicunas living in families with adjacent neighbors with vicunas living in families without neighbors (CM)

Values for each category are given in tables 1 and 5

Behavioral category	Male	Female
Graze	PG < CM	PG < CM
Lookup	PG > CM	PG > CM
Alert	PG = CM	PG < CM
Lie	PG = CM	PG = CM
Roll	PG = CM	PG = CM
DU	PG = CM	PG = CM
Walk	PG = CM	PG > CM
Run	PG > CM	PG = CM
Chase	PG > CM	
Threat	PG > CM	PG > CM
Standoff	PG > CM	
Groom	PG = CM	PG = CM

Significance level, $p < 0.05$, Kruskal-Wallis ANOVA.

Behavior and proximity to neighbors

The presence of neighbors had a significant effect on the time budget of males during the mating season (Tabs. 5, 6). At Pampa Galeras (PG), resident males defended boundaries to territories that abutted two or three other territories. In addition, there were several bachelor groups using the area that intruded on the resident's territories. Each resident male monitored the position of its neighbors during the day and watched for intruders. At the Coppermine site (CM), the territories of resident males did not abut other territories. The nearest neighbors were out of sight, and no bachelor groups were present during the study. Males without neighbors grazed more and spent less time performing behaviors that repelled intruders. There was no significant difference in the time budgets for females at high or low density sites except for "alert". Females spent more time in "alert" at the high density site.

The differences in behavior between males and females observed at the high-density Pampa Galeras site were also evident at the low-density Coppermine site (Tab. 6). Males spent more time than females walking about, visiting dung piles and boundaries, and in "look up" and "alert". Males recognized a boundary to the territory whether or not neighbors were present, and differences in behavior were quantitative not qualitative.

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Zusammenfassung

Über das Verhalten von Vikunjas (*Vicugna vicugna* Molina, 1782). Unterschiede bedingt durch Geschlecht, Jahreszeit und Entfernung zu Nachbarn

Das Verhalten von erwachsenen, männlichen Vikunjas unterschied sich quantitativ und qualitativ vom Verhalten der erwachsenen, weiblichen Vikunjas, und dieser Unterschied bestand während und außerhalb der Brunstzeit. Weibchen verbrachten mehr Zeit beim Grasen, während Männchen sich anderweitig beschäftigten. Das Verhalten der Männchen war auf Wachsamkeit gerichtet, das Vertreiben von Eindringlingen und die Markierung ihres Gebietes. Dieses Verhalten war jedoch häufiger während als außerhalb der Brunstzeit. Gebietstreue Männchen verteidigten ihr Gebiet das ganze Jahr über. Weibchen halfen dabei nie. Die Anwesenheit eines fremden Männchens erhöht die Verteidigungsbereitschaft der gebietstreuen Männchen. Dieses hatte jedoch keinen Einfluß auf das Verhalten der Weibchen.

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